PIGMENT MIGRATION AND LIGHT-ADAPTATION IN THE EYE OF THE MOTH, GALLERIA MELLONELLA[1]

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With few exceptions, the compound eyes of arthropods fall into two groups—those with relatively short rhabdoms and pronounced migrations of accessory shielding pigment, and those with rhabdoms extending the length of the retinulae and little or no movement of pigment (Exner, 1891). The former occur in nocturnal animals or species which are found where there is low illumination; the second type is characteristic of diurnal forms which are active where there is ample light.

Because of this ecological correlation it has been widely assumed since the time of Exner that migratory pigment is an adaptation for vision in dim light; however, physiological evidence in support of this view has been provided only recently. The eyes of moths dark-adapt in two steps, but the second, slower phase does not, as in the human eye, represent a second population of receptors with lower thresholds. The increase in sensitivity of the eye during this slow phase runs parallel with the migration of shielding pigment as it moves distally to a compact mass between the crystalline cones (Bernhard and Ottoson, 1960a, 1960b, 1964; Bernhard, Höglund and Ottoson, 1963). Eyes which have no migratory pigment lack the second component in the dark-adaptation curve (Bernhard and Ottoson, 1960a; Bernhard, Höglund and Ottoson, 1963; Goldsmith, 1963), and in the fully dark-adapted state they are not as sensitive as eyes in which the pigment sleeves have withdrawn distally (Bernhard, Höglund and Ottoson, 1963). Compound eyes with short rhabdoms and migratory pigment can appropriately be called *scotopic* eyes; those with no migratory pigment, *photopic*.[3]

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[3] A brief consideration of terminology is necessary here. The traditional names for these types of compound eye are superposition and apposition, and were introduced by Exner (1891). These terms refer to supposed differences in refractive properties and mode of image formation which Exner described in great detail but which subsequently have been shown not to be general properties of the two groups (Kuiper, 1962; Goldsmith, 1964). The *raison d'être* of these names is thus rooted in an erroneous analysis of the optics of compound eyes, and the only argument for perpetuating them is that they have existed now for almost three-quarters of a century. We feel they should be replaced by terms that relate to the known properties of the eyes and that are established in the vocabulary of visual physiology. By scotopic eye we thus mean one which is of the morphological type which was supposed by Exner to form superposition images and which is adapted (in an evolutionary sense) for high sensitivity in dim light. Obviously the basis for this adaptation—migratory shielding pigment—is different from scotopic vision mediated by a rod-rich vertebrate retina. There remains a relatively small number of compound eyes with the photopic (apposition) morphology but which possess migratory pigment. What their proper physiological place may be must await experimental analysis.

In many Lepidoptera light controls migrations, either by direct action on the pigment cells or indirectly through the sense cells; the most recent work indicates that pigment migrations can be observed in isolated retinas and that connection with the optic ganglion or the circulation is not necessary (Tuurala, 1954). In such moths, cold or narcosis causes the pigment to move to the light-adapted position (Day, 1941), suggesting that the process which holds the pigment in the dark-adapted state requires metabolic energy and that possibly the effect of light is to inhibit this process.

The first part of this paper is a quantitative study of the light energy and time necessary to effect pigment migration in the scotopic compound eye of the wax moth, *Galleria mellonella*. The second part deals with the rate of light adaptation and how it is influenced by the presence of migratory pigment.

I. THE CONTROL OF PIGMENT MIGRATION BY LIGHT

Methods

Intact moths (*Galleria mellonella*) were placed on their backs and secured to a small cork platform with soft wax ("Tackiwax"). After a minimum of one hour dark-adaptation the animals were exposed to an adapting light for varying lengths of time.

The adapting light was obtained with a high-pressure xenon arc and a Bausch and Lomb grating monochromator, and consisted of a narrow band of wave-lengths (10 $m\mu$ half band width) centered at 500 $m\mu$. An image of the diffraction grating was focused on the animals' heads. Intensity was controlled with a pair of calibrated optical wedges. Energy flux was measured with an Eppley bismuth-silver thermopile of known sensitivity and a Keithley No. 149 millimicrovoltmeter.

After a specified exposure the animals were decapitated under dim red light, the heads bisected, and the halves placed in Duboscq-Brasil fixative in the dark for 12–16 hours. The tissue was dehydrated and imbedded in paraffin by standard techniques. Sections 10 μ thick were cut parallel to the ommatidial axes, cleared of paraffin, and examined without staining with a phase contrast microscope to assess the extent of pigment migration. Some sections were depigmented with Grenacher's solution and stained with Harris's haematoxylin to aid in orientation.

Pigment position was measured as the distance between the distal end of the crystalline cone and the proximal border of the secondary pigment (see Fig. 1); but in order to compare eyes of different sizes, this figure was expressed as a fraction of the distance from the cone to the basement membrane. For ease in understanding, this index has been expressed in Figures 2 and 3 as a percentage of the total possible migration observed in eyes exposed to direct sunlight.

Experiments were performed in midafternoon during the months of June, July, and August, with animals reared in the laboratory by the method of Dutky, Thompson and Cantwell (1962).

Results

Figure 1 shows the positions of the pigment in dark- and light-adapted eyes. The nuclei of the retinular cells, which are located in the distal processes and are not readily visible in Figure 1, also migrate proximally in the light.

The extent of pigment migration after 3 and 27 minutes irradiation is shown in Figure 2 as a function of incident energy. Not only does the pigment move farther the higher the energy, but for each flux the pigment migrates more in 27 minutes than in three.

These conclusions are amplified by Figure 3, which shows the time course of migration for two intensities of light. In each case migration starts immediately at a relatively high rate, then slows as the pigment reaches a steady-state position characteristic of the incident energy. The time required to attain the final steady-state position is longer the farther the pigment moves and is of the order of half an hour for the nearly complete migration produced by 5×10^3 ergs sec.$^{-1}$ cm.$^{-2}$ at 500 mμ.

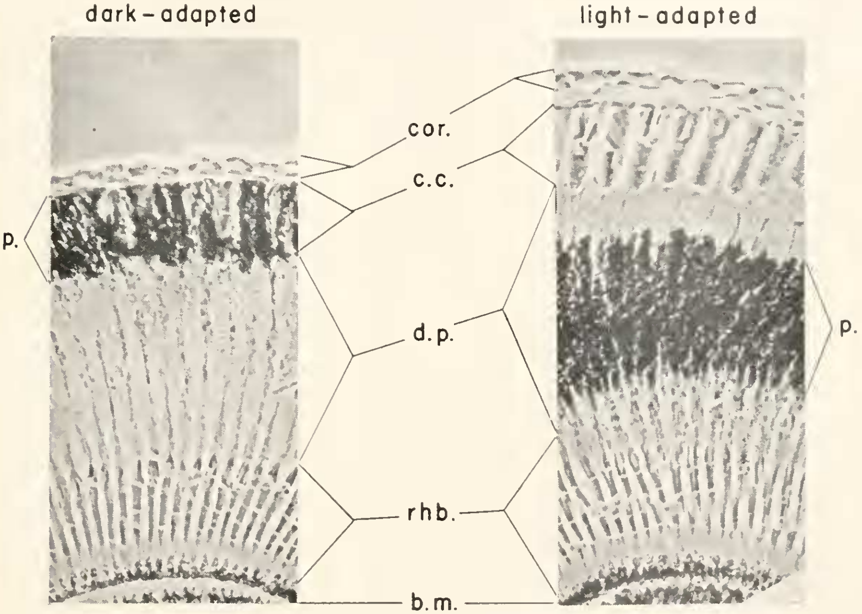

FIGURE 1. Sections of *Galleria* eyes cut approximately parallel to the long axes of the retinulae and showing the positions of the migratory pigment in the fully light- and dark-adapted states. The nuclei of the retinular cells, which are in the distal processes but are not readily visible without staining, also migrate distally in the dark. Sections were unstained and were photographed with phase-contrast optics. As a scale reference, the cystalline cones are about 45 μ in length. *Cor.*, cornea; *c.c.*, crystalline cone; *d.p.*, distal processes of the retinular cells; *rhb.*, rhabdoms; *b.m.*, basement membrane; *p.*, migratory pigment of the secondary pigment cells.

Discussion

Eyes exposed to the same combinations of intensity and time frequently show wide variation in pigment position; consequently a great many sections must be prepared to achieve a high precision of measurement, and this has discouraged us from measuring an action spectrum by this histological procedure.

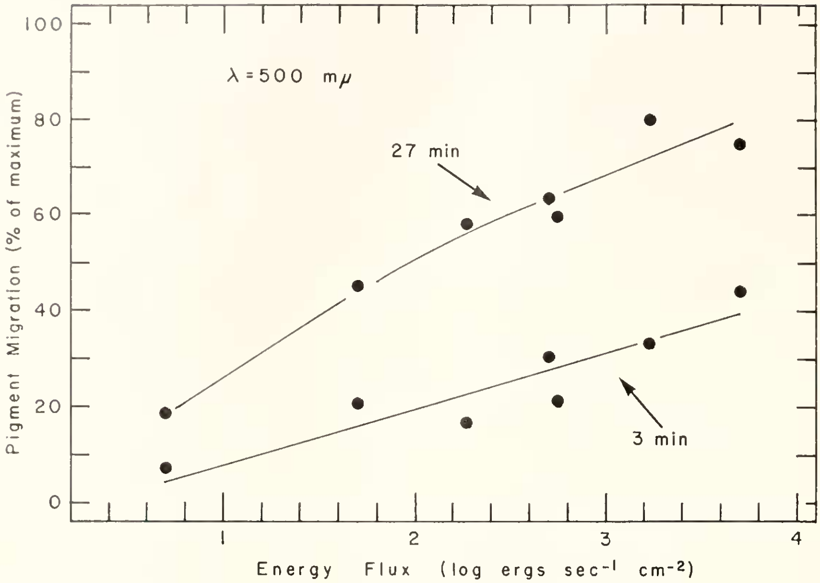

FIGURE 2. Proximal pigment movement as a function of energy for two different times of exposure, as determined from histological sections similar to those in Figure 1. Each point represents the average of about a dozen measurements on several sections from at least two eyes, each from a different moth. Energy flux was measured with a thermopile at the surface of the cornea. Wave-length was 500 mμ.

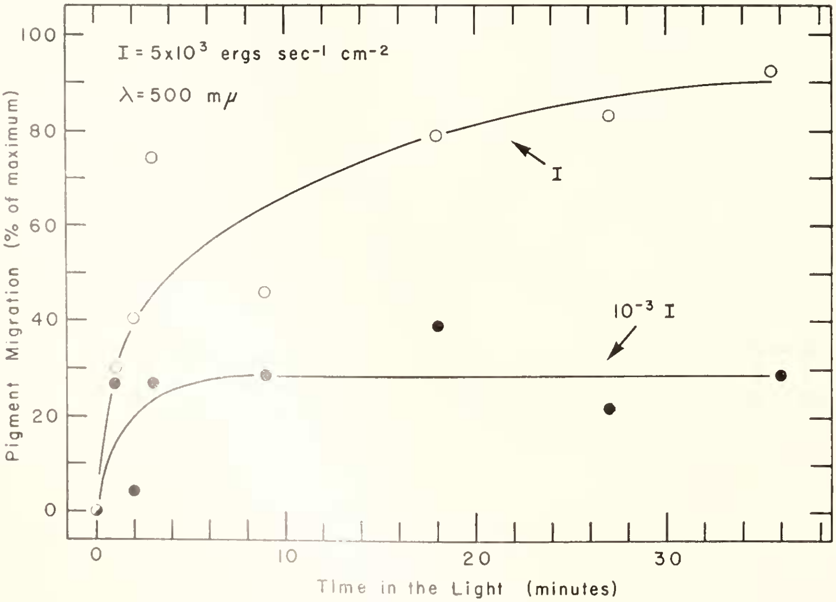

FIGURE 3. Proximal pigment movement as a function of time in the light. Details as in Figure 2.

The controlling effect of light is not all-or-none, for the extent of migration is a function of intensity. This is consistent with the thought that the rate of a chemical reaction necessary for the pigment to be held in the distal (dark) position is slowed by light, but a more precise kinetic model cannot be tested critically on the basis of the experimental observations presently available.

The finding that the pigment assumes intermediate positions in the presence of dim lights is in agreement with recent work of Bernhard and Ottoson (1964) who observed in *Cerapteryx graminis* a partial retraction of pigment towards the dark position when the intensity of a steady adapting light was decreased but not extinguished completely. Our observations on the time course of pigment movement are in semiquantitative agreement with Höglund (1963a), who reports that the large area of glow characteristic of dark-adapted eyes of various nocturnal Lepidoptera becomes minute when the pigment occupies a position intermediate between the distal and proximal extremes; and further, that glow requires 10 minutes or more to disappear when the eye is exposed to light. In a later paper Höglund (1963b) shows a case in which glow has vanished in less than 5 minutes. Both of these times are in reasonable agreement with our results, considering that different species were studied and that there is no precise information on Höglund's adapting energies or the relation between pigment position and the point at which glow vanishes.

II. The Rate of Light-Adaptation

Bernhard and Ottoson (1960a, 1960b, 1964) and Bernhard, Höglund and Ottoson (1963) have shown that dark-adaptation of moths has two components which, under some conditions, are completely separated in time. The second phase is caused by the distal migration of the shielding pigment and produces a fall in threshold of the eye of 1–3 log units. It does not indicate an intrinsic change in sensitivity of the retinular cells, but rather an increased probability that light crossing the cornea will reach the receptors (Höglund, 1963b).

The correlation between sensitivity change and pigment position during dark adaptation of scotopic eyes prompted us to examine the corresponding relationship during light-adaptation. A photopic compound eye lacks both pronounced pigment migration and the slow phase of dark adaptation (Bernhard and Ottoson, 1960a, 1960b; Bernhard, Höglund and Ottoson, 1963). Moreover, the rate of light-adaptation—measured as the change in increment threshold in the presence of the adapting light—is very rapid; a steady value of sensitivity is achieved within seconds after turning on the adapting light (Goldsmith, 1963). On the other hand, in a scotopic eye where pigment moves for minutes after exposing a dark-adapted eye to the light, one might, at least on first thought, suppose that light-adaptation should be correspondingly extended in time and increased in extent. The following experiments are in agreement with Höglund (1963b) in showing that this expectation is—for good reason—usually not fulfilled, but they indicate a greater variety in the shapes of light-adaptation curves than is suggested by his short but excellent paper.

Light adaptation curves of scotopic compound eyes have a multiple origin. There is a rapid fall in sensitivity as the receptors adjust their thresholds to the adapting light, but with the inward migration of pigment there are two additional effects which are opposed to one another. The test light reaching the receptors is attenuated, and this leads to a further *fall* in sensitivity of the *eye;* however, the adapting light is also decreased by the same pigment screen, and this permits the *receptors* to *gain* sensitivity. This was shown (Höglund, 1963b) by conducting the light stimulus to the receptors through a glass fiber inserted below the pigment, but we have come to the same conclusion from different experimental evidence. Rapid light-adaptation in the presence of pigment migration therefore means that the effect of attenuation of the test flash by the shielding pigment is approximately balanced by dark-adaptation of the receptors.

Methods

Optical. The test and adapting lights were 6-v. tungsten filament microscope lamps placed in light-tight metal boxes fitted with camera shutters. For most experiments the light paths originated at right angles to each other; they were combined with a beam splitter and arrived at the cornea on the same optical path. In some experiments a second test light was arranged so as to stimulate the eye from another angle.

Intensity of the test light was controlled with a circular optical wedge, and the adapting light with neutral density filters. In the experiments described below, intensity of the adapting light was sufficiently great to move the pigment to the proximal position. Infrared was attenuated with 1.25 cm. of a 10% (w/v) copper sulfate solution. Duration of the test exposures was monitored with a photocell.

Recording. Animals were immobilized in soft wax at the focus of the light beams. A shield of aluminum foil prevented light from reaching parts of the animal other than the illuminated eye. The retinal action potential was recorded with silver:silver chloride electrodes which made contact with the animal through a Ringer-filled capillary with a tip diameter of about 20 μ placed beneath the cornea of the illuminated eye, and a saline-soaked wick on the dark side of the head. The Ringer was that of Ephrussi and Beadle (1936). The responses were recorded with a direct-coupled amplifier (Grass P-6) and photographed from the face of an oscilloscope.

Analysis. A series of responses to increasing intensities was recorded for the dark-adapted eye and whenever the animal was held for an extended period in a light-adapted state. The test flashes were 0.5 sec. The height of the sustained negativity was plotted as a function of log I. Response-energy curves for the light-adapted eye were parallel, or nearly so, to those obtained from the dark-adapted eye, as found in other moths by Bernhard and Ottoson (1960a). Their displacement on the energy axis gives the change in sensitivity of the eye.

During light- and dark adaptation the eye was stimulated every ten or more seconds with a test flash of constant intensity. The shifting position of the response-energy curve, and thus the changing sensitivity of the eye, was determined by comparing the size of each potential with the response-energy curve for the dark-adapted eye (*cf.* Hartline and McDonald, 1947; Goldsmith, 1963). For the measurement of dark-adaptation, test flashes were chosen that could be presented to the completely dark-adapted eye at 10-second intervals without themselves producing light-adaptation.

Adaptation measurements are usually presented in terms of threshold rather than sensitivity. The term log relative threshold is used below synonymously with

-log relative sensitivity. It corresponds to the log of the intensity required for a constant effect.

Twenty-three animals were studied.

Results and Discussion

Figure 4 shows that dark-adaptation of *Galleria mellonella* sometimes splits into two components. As shown by the more typical recovery curve in Figure 5, however, this is a species in which the two limbs of the curve are usually not distinct.

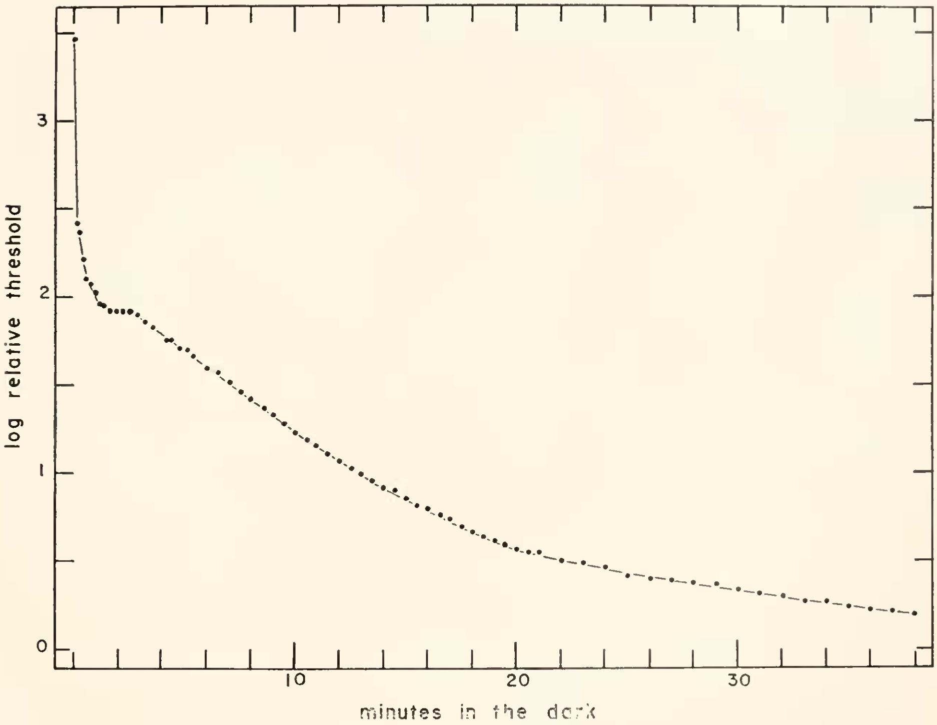

FIGURE 4. Dark-adaptation of the compound eye of *Galleria mellonella* in an animal showing a distinct latency before pigment migration started.

Overlap of pigment migration with physiological recovery has also been observed in other species (Bernhard, Höglund and Ottoson, 1963). It means that following the extinction of the adapting light the dark migration of pigment has commenced with little or no latency. The important point, however, is that dark-adaptation of *Galleria* is increased in extent and prolonged in time by the presence of migratory shielding pigment, just as in other species studied by the Swedish workers.

Not so light-adaptation. At least usually not; we shall consider exceptions in due course. Figure 6A (filled circles) shows the abrupt rise in threshold of an initially dark-adapted eye as a function of time after turning on a steady adapting light. Within seconds the sensitivity has reached its final value, even though the histological observations of pigment movement indicate that migration requires minutes for completion.

Figure 6A also shows that the wave form of the retinal action potential changes with time. The significance of this observation can be clarified by examining how the same eye responded when dark-adapted and stimulated by a series of flashes of increasing intensity (Fig. 6B). Ganglionic components are small and are most evident at low intensities and at "on"; the response is dominated by a graded potential which rises slowly and persists as long as the stimulus. With increasing intensity the rate of rise increases. At high intensities, instead of rising smoothly to a plateau there is an initial peak, about 100–200 msec. duration and graded with intensity, preceding the final steady value. This initial peak is evident in the response to the brightest light (log $I = 0$). Evidence of other kinds, including intracellular recording, suggests that both the initial peak and the plateau arise in the retinular cells (see Ruck, 1962 for review); for present purposes, however, it

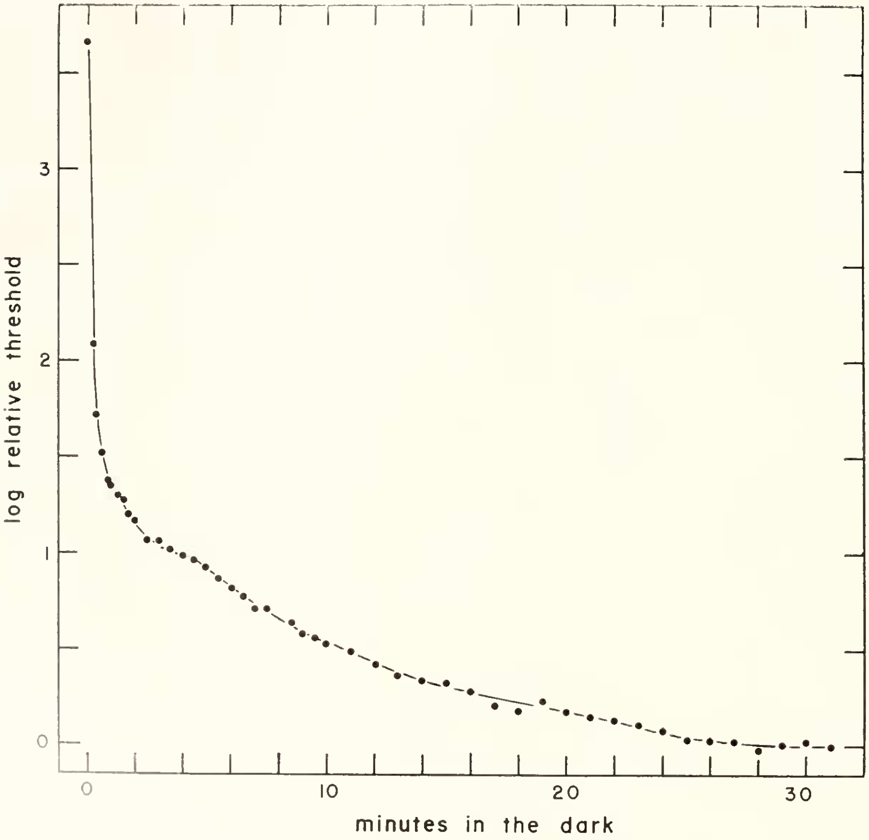

FIGURE 7. A more typical dark-adaptation curve than Figure 4, showing that in this species pigment migration usually overlaps the earlier, faster components of recovery.

is sufficient to note that the initial peak is observed only when the cells are illuminated strongly.

The test flash used for the light-adaptation in Figure 6 was log $I = -1$, which produced a barely perceptible initial peak in the dark-adapted eye. On turning on the adapting light the response was decreased, but the initial peak became more prominent relative to the plateau (*cf.* responses at 0 and 24 sec.). The latter is the expected result of having more light—*i.e.*, both beams—incident on the receptors.

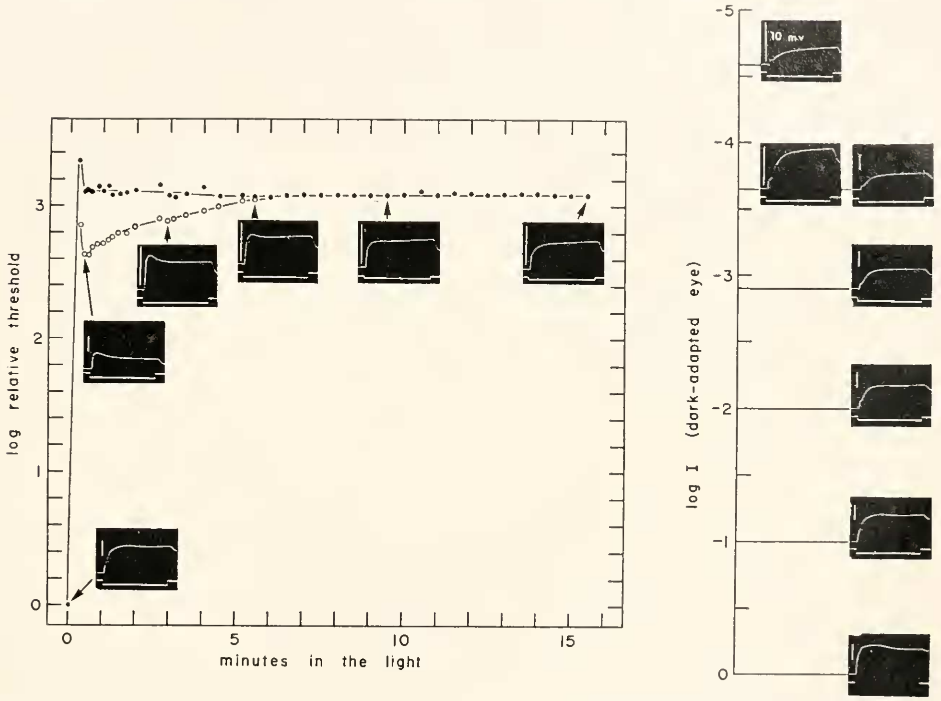

FIGURE 6. Light-adaptation of a compound eye of *Galleria*. Filled circles, based on the maintained plateau of the retinal action potential; open circles, based on the greatest excursion of the response. Several of the oscillograms from which the experimental points were calculated are included with the curve to show the progressive change in wave form of the retinal action potential during light adaptation. To the right of the graph is a series of responses to different intensities of stimulation recorded from the same animal while the eye was dark-adapted, just prior to irradiating with the adapting light. Test flashes were 0.5 sec. duration; a 10 mv. calibration mark is included with each trace.

The change in shape of the electrical response poses a problem: should one calculate sensitivity on the basis of the plateau or the highest part of the wave form? It is not obvious which is most important at the first synapse, so the issue has been avoided in Figure 6 by plotting both results. The filled circles are determined from the plateaus; the open circles are based on the greatest excursion of the response, which in the early minutes was the initial peak. By six minutes the peak had subsided, however, and the two light-adaptation curves meet. Even between 9.5 and 15 minutes, though, the form of the response continued to change; the height of the response remained constant, but its rate of rise decreased.

These progressive changes in the shape of the retinal action potential are characteristic of decreasing intensities of stimulation. They can be accounted for by a gradual diminution of the light reaching the receptors caused by the proximal migration of shielding pigment. The pigment is known to be moving during this time, even though the sensitivity of the eye is constant.

That attenuation of the test and adapting lights should produce equal and opposite effects on the sensitivity of the eye is a consequence of two factors: (a) equal absorption by the screening pigment, and (b) the applicability of Weber's law at the level of the retinal action potential. Insofar as the test and adapting beams are coaxial, for each position of pigment, absorption of the two lights will be the same. When the intensity of the test light reaching the receptors is decreased by the pigment screen to 0.1 of a previous value, clearly the energy in the flash will have to be increased ten-fold to maintain a constant response from the receptors; that is, sensitivity of the eye will have *fallen* one log unit. But if $\Delta I/I$ (ratio of incremental threshold to adapting intensity) is constant, at least over a significant range, the fall in intensity of the adapting light will produce an exactly equivalent *increase* in sensitivity of the receptors. Writing Weber's law,

$$\frac{\Delta I}{I} = \frac{I_t - I_a}{I_a} = k$$

where I_t and I_a are the intensities of the test and adapting lights, one can see that

$$I_t = I_a(k + 1)$$

$$\log I_t = \log I_a + \text{const.}$$

In other words, the curve log I_t *vs.* log I_a has a slope of unity (except close to threshold where the simple form of Weber's law used here must be modified), and a decrease of one log unit in I_a will produce an increase of one log unit in the sensitivity of the eye (Fig. 8).

Such rapid rates of light adaptation as shown in Figure 6A are not always observed. Figure 7 compares the light adaptation of two other animals, one rapid, the other much slower. Both curves come within 0.2 log unit of the same final value and are based on the plateau of the retinal action potential. Other animals light-adapted at intermediate rates.

The problem is not why the time course of light-adaptation is usually rapid in scotopic eyes, but why it is relatively slow in some. A slow rate of light-adaptation means that for each position of pigment (a) the test flash is attenuated more than the adapting light or (b) the decrease in energy of the adapting light fails to produce an equal dark-adaptation of the receptors. We shall consider each of these possibilities in turn.

What might be expected from unequal absorption of the test and adapting lights? After the initial rise in threshold observed during the first few seconds, further changes will depend on appropriately weighted averages of the optical

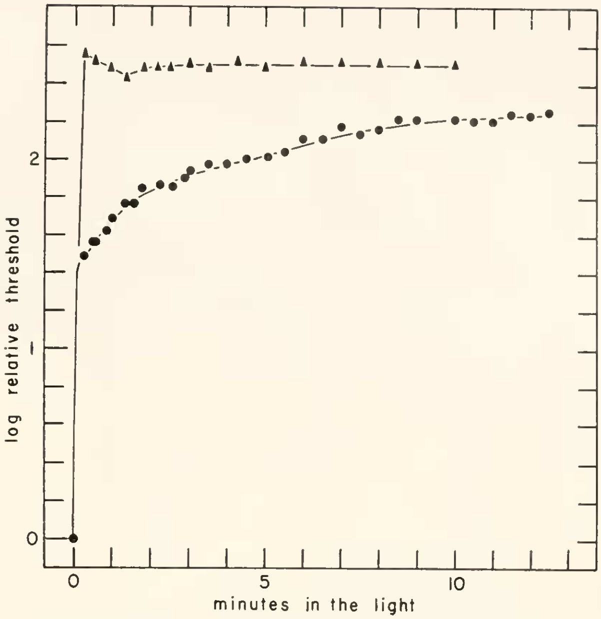

FIGURE 7. Light-adaptation of two eyes, illustrating the variation in rate which is observed in different animals. Both curves are based on the height of the plateau in the retinal action potential.

densities of the light paths in front of the receptors:

$$\log \text{recovery} \propto \text{O.D. of adapting path}$$
$$\log \text{rise in threshold} \propto \text{O.D. of test path}$$

Consequently,

$$\Delta \log \text{threshold} = (\text{O.D. test path}) - (\text{O.D. adapting path}).$$

This difference in optical densities will vary as a function of time until pigment migration is complete.

With coaxial beams it is not obvious how either light could be selectively screened, for both beams entered the eye along the same path. Nevertheless, in the hope of accentuating a selective absorption we have performed several experiments with one or the other of the beams impinging on the eye obliquely. When the test light strikes the pigment screen obliquely and the adapting light enters more or less axially, the O.D. of the test path will likely be greater than the O.D. of the adapting path, and Δ log threshold will continue to rise until the pigment has reached the proximal position. On the other hand, if the adapting light is oblique and the test light axial, the difference in O.D. will be negative and log threshold should fall somewhat. When the optical densities are equal (coaxial beams) there will be no further change in threshold irrespective of pigment position.

Of three experiments with an oblique test light, adaptation was very slow in two but essentially instantaneous in the third. In three experiments with an oblique adapting light the threshold rose to a maximum but did not subsequently decrease. In two of these animals the time course was rapid, but in the third it was slow. In these experiments there is therefore no clear demonstration of the effects that are expected as a result of differential absorption.

The most convincing experiments, however, are two in which light-adaptation was measured with a pair of test flashes presented alternately at intervals of several seconds, one oblique and a second coaxial with the adapting beam. These are shown in Figure 9. In each case the change in sensitivity to the axial test light was greater than to the oblique test light. This means that the populations of receptors responding to the two test lights were not identical and that the adapting light did not have an equal effect everywhere in the eye. In each experiment the time courses of adaptation were the same with the two test lights, and in one experiment they were very rapid. The difference in the shapes of the light-adaptation curves clearly depends on something other than the geometric arrangement of stimulating and adapting lights. Thus, under the conditions of these experiments there is no evidence for preferential absorption of either beam.

This brings us to the second possibility—that under some conditions there is an asymmetry in the physiological *effects* of decreased test and adapting lights. For example, attenuation of the adapting light might be more rapid than the ensuing equivalent recovery of the receptors. This could be observed if in some individuals resynthesis of visual pigment or some other physiological component of recovery were unable to keep pace with the proximal migration of screening pigment, either

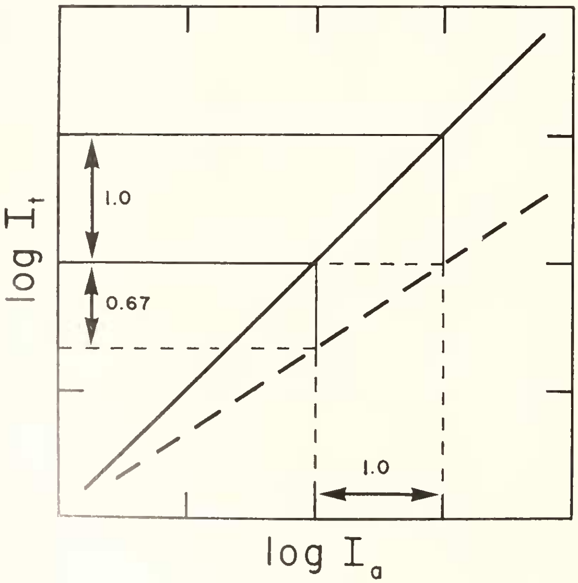

FIGURE 8. Solid curve: part of the increment threshold function for a photoreceptor which obeys Weber's law. A decrease in the adapting intensity leads to an equal recovery of the receptor. Broken curve: part of the same function for a receptor in which a drop of adapting intensity of 1.0 log unit produces only a 0.67 log unit fall in the increment threshold. See the text for a discussion.

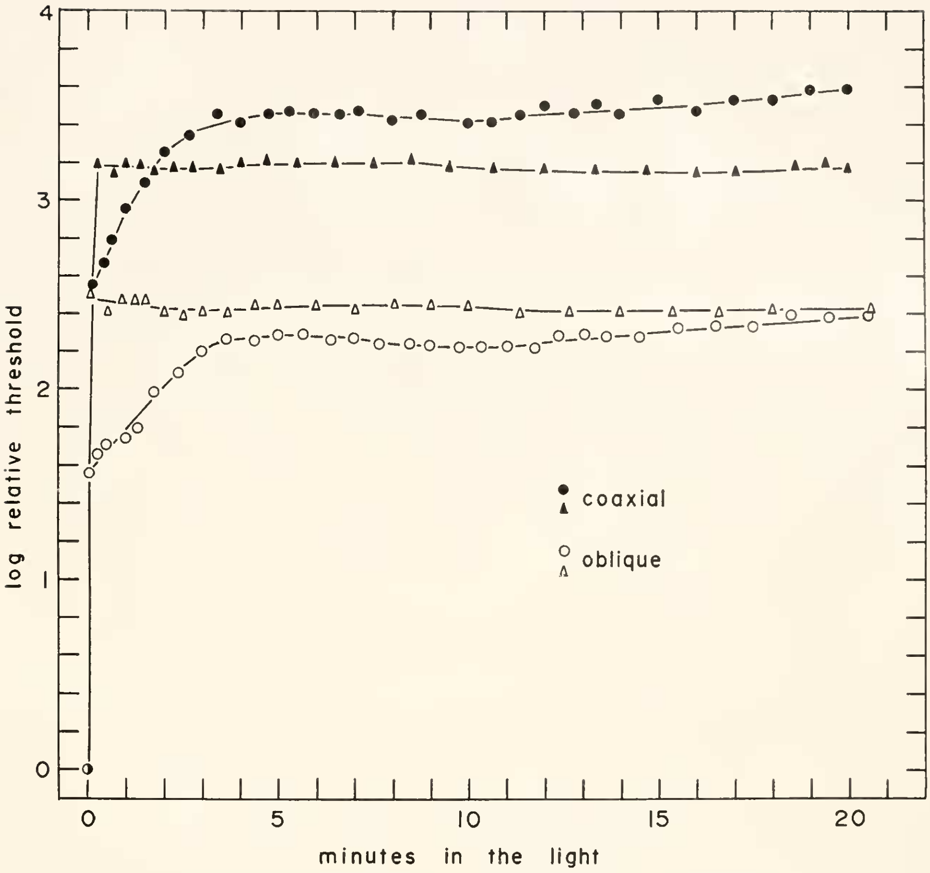

FIGURE 9. Pairs of light-adaptation curves for two animals (circles and triangles). Each pair of curves was measured during the same adapting exposure by stimulating the eye alternately with test flashes coaxial with the adapting beam (filled symbols) and obliquely (about 70°) to the adapting beam (open symbols). One animal (triangles) light-adapted much more rapidly than the other, irrespective of the angle between the test and adapting lights. All curves were based on the plateau in the retinal action potential.

because the former were unusually slow or the latter unusually rapid. If such were the case, *slow* light-adaptation would be observed in eyes with the *fastest* rates of pigment movement. Whether these rates vary sufficiently to account for the different rates of light-adaptation which have been observed is not known. Judging from the speed of dark-adaptation of photopic eyes, however, it seems unlikely that recovery of the receptors of scotopic eyes would lag behind movement of the pigment.

Alternatively, attenuation of the adapting light might not be followed by an equal dark-adaptation. If the increment threshold function, plotted as log I_{test} *vs.* log I_{adapt}, had a slope less than 1.0, partial dark-adaptation of the receptors caused by screening of the adapting light would not completely offset the rise in threshold caused by attenuation of the test light (Fig. 8). Measurements of this slope in seven animals gave values ranging from 1.0 to 0.67. The mean was 0.88 with a standard deviation of ±0.16, and the distribution was skewed toward lower values. In each case the measurements were made over approximately the same range of intensities. In the animal which provided the smallest value, attenuation of the test and adapting light 1 log unit by screening pigment would permit the receptors to recover only 0.67 log unit, and a slow component of light-adaptation covering 0.33 log unit might be expected to occur as pigment moved inward. The maximum range over which pigment controls sensitivity during dark-adaptation is about three log units (Bernhard and Ottoson, 1964). Making the most generous allowance which is justified by present evidence, therefore, a slow component of light-adaptation based on a non-linear relation between ΔI and I might be expected to cover as much as one log unit. With the possible exception of two animals, all of the moths studied did not exceed this value. In the two apparent exceptions, light adaptation was not followed by a control dark-adaptation, so that the possibility of physiological deterioration cannot be eliminated.

The experiments reported here lend support to the view that the presence of migratory shielding pigment in the compound eyes of arthropods extends the dynamic range of these eyes and is an adaptation for vision under scotopic conditions.

We are grateful to Mrs. Wiliam Palumbo for her skillful assistance, particularly with the histology; to Dr. Raimon Beard for several gifts of *Galleria* stock; and to Nathan Mandell for aid in the construction of equipment.

SUMMARY

1. An energy flux at the cornea of 5×10^3 ergs sec.$^{-1}$ cm.$^{-2}$ at 500 mμ causes almost complete migration of the accessory shielding pigment in the eye of the wax moth, *Galleria mellonella*. Movement requires approximately 30 minutes. Lower energies bring the pigment to steady-state positions intermediate between the fully light- and dark-adapted positions.

2. Light-adaptation, unlike dark-adaptation, runs a faster time course than pigment migration and is frequently complete in several seconds. This confirms an earlier report of Höglund. The theoretical reasons for a rapid rate of light-adaptation in the face of slow pigment migration are discussed and are shown to be a consequence of (a) equal absorption of the test and adapting lights by the sleeves of accessory pigment, and (b) a linear relation between ΔI and I.

3. It is suggested that the terms, superposition and apposition eye, be replaced by scotopic and photopic eye, as the latter indicate more accurately the physiological properties of these photoreceptors.

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